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Catch-per-unit-effort and size spectra of lake fish assemblages reflect underlying patterns in ecological conditions and anthropogenic activities across regional and local scales

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Abstract

Across broad geographic scales, ecological indicators for fish assemblages should represent causal ecological processes, be sensitive enough to show patterns across the landscape, and reflect underlying biotic or abiotic conditions that influence those patterns. We assessed the responses of commonly applied ecological indicators for lake fish assemblages: mean body size, catch-per-unit-effort (CPUE), and normalized length size spectrum (NLSS) slope to regional (climate, water chemistry, and watershed stress due to human activities) and local (lake morphometry, water quality, and angling pressure) ecological and anthropogenic variables. The indicators were estimated using fish assemblage catch data acquired via a standardized gillnetting protocol implemented within 693 lakes in Ontario, Canada. To our knowledge, our study is the first size-based or catch-based indicator evaluation to include detailed observations of angling pressure on hundreds of inland lakes. Boosted regression tree models showed that CPUE of large-bodied organisms and NLSS slope best described underlying patterns in the regional and local variables. Models developed with a mix of regional and local variables performed better than models developed with regional or local variables alone. The relative influences of the variables and responses varied among indicators but in general, ecological variables had greater influence on the indicators than anthropogenic variables. These results emphasize the complex and multi-scaled nature of factors and ecological processes affecting body size, habitat-community production, and trophic dynamics in lake fish assemblages.

Key words: fish assemblages, ecological indicators, lakes, size spectrum, ecological and anthropogenic gradients

Introduction

The composition and production of fish assemblages in lakes of the northern hemisphere are shaped by large-scale processes and factors such as postglacial re-colonization, geomorphology, and climate. They are also influenced by small-scale, local factors such as lake morphometry, water quality, angler harvest and biotic interactions (Tonn 1990; Jackson et al. 2001). All of these factors combine to create a mosaic of lake types, fish assemblages, and fisheries resources that vary across spatial gradients. Temporal gradients in fish production also occur in response to seasonal, inter-annual and longer-term (e.g., North Atlantic Oscillation) fluctuations in environmental conditions.

Recreational anglers who exploit these resources also vary their angling pressure in space and time. In Ontario, recreational angling commonly occurs in streams and lakes within 1 km of a road, but anglers can drive an average of 290 km per trip to access lakes. Therefore, lakes closer to human settlements receive greater levels of angling pressure than lakes farther away (Drake and Mandrak 2010; Hunt et al. 2011). Angling pressure also fluctuates in time with more pressure on weekends, and peaks during the summer open water and winter ice fishing seasons.

Given the variation in lake types, fisheries resources, and angling pressure across broad geographic areas, recent papers have suggested that management of lakes and the recreational fisheries they support should occur at the landscape rather than traditional individual lake level (Lester et al. 2003; Post 2013). Furthermore, individual lake approaches have led to complex fisheries regulations that require vigilance from anglers and do not account for shifting pressure as restrictions on preferred lakes may increase pressure on adjacent lakes (Lester et al. 2003; Post et al. 2008). The landscape approach advocates setting biological achievable targets, periodic

state of the resource monitoring, and adaptive management at the regional scale (Lester et al. 2003).

Integral to reporting and evaluating the state of fisheries resources is the identification of ecological indicators that respond to variations along environmental and/or disturbance gradients (Karr and Chu 1997; Jennings and Dulvy 2005). Fishes and particularly, top predators have been used as ecological indicators in lakes because they are relatively easy to sample, and they have commercial and aesthetic value. Also, their ecology is well-understood so changes in individual, population or community dynamics can be related to direct and indirect effects of environmental conditions or stressors (Cairns et al. 1993). A myriad of indicators exist for fish ranging from individual indicators such as growth or body condition to ecosystem level indicators such as nutrient cycling or trophic diversity (Mark et al. 2003; Jennings and Dulvy 2005; Emmrich et al. 2011). Three such indicators, which were the focus of our study, are mean body size, catch-per-unit-effort (CPUE), and normalized length size spectrum (NLSS).

Mean size and CPUE comparisons are important because they reflect fundamental physiological and ecological processes shaping respiration, growth, maturation and abundance in fish assemblages (Jennings and Dulvy 2005; Emmrich et al. 2014). To attain these types of data, many fish community monitoring programs worldwide use benthic multi-mesh gillnets deployed throughout study lakes using standardized sampling designs (Bonar et al. 2009; Sandstrom et al. 2011; Emmrich et al. 2011). Comparisons of mean size and CPUE of these types of data have been used to compare body size along temperature gradients (Emmrich et al. 2014), compare fish community composition based on morphometric and trophic status (Diekmann et al. 2005), and assess the effects of invasive species, human exploitation, and anthropogenic substances on fish assemblages (see Guzzo et al. 2014).

In aquatic ecosystems, large predators eat smaller prey and empirical evidence across taxonomic and functional groups show consistent patterns of decreasing abundance with body size (Sprules and Munawar 1986; Petchey and Belgrano 2010). Based on these patterns, normalized biomass size spectrum (NBSS) and normalized length size spectrum (NLSS) have been advocated in the literature as simple ataxonomic metrics that represent underlying size-dependent, biological processes of predation, growth, and respiration that structure aquatic assemblages (Sprules and Munawar 1986; Kerr and Dickie 2001; Emmrich et al. 2011; Gómez-Canchong et al. 2013). Commonly calculated using least-squares linear regression between log-transformed values of body size (on the x -axis) and abundance (on the y -axis) within body size bins, size spectra are characterized by the estimates of intercept and slope (Gómez-Canchong et al. 2013). The intercept can indicate total or standing stock biomass (Sprules and Munawar 1986; Boudreau and Dickie 1992) while the slope represents ecosystem structure, i.e., the relative contribution of small versus large organisms, which result from underlying energy transfer efficiency and predator-prey size ratios (Sprules and Munawar 1986; Gómez-Canchong et al. 2013; Yurista et al. 2014). Normalized biomass size spectrum slopes are expected to be around -1 to -2 depending on whether biomass or number of organisms are used represent density (Andersen and Beyer 2006; White et al. 2008; Basset and Sabetta 2009) (Fig. 1). The expected slope from NLSS whereby body size is characterized by length as opposed to weight, is -6 based on the length-weight relationship; $W=L^3$ where W is weight and L is length (Fig. 1). Normalized biomass size spectrum and NLSS slopes have been used to relate fish assemblages to the environmental conditions of lakes, and quantify the impacts of perturbations such as pollution, habitat modification or fisheries exploitation (Shin and Cury 2004; Emmrich et al. 2011; Gómez-Canchong et al. 2013).

Although mean body size, CPUE and size spectrum slope are recognized ecological indicators (Emmrich et al. 2011), their capacity to reflect broad-scale patterns in regional and local ecological and anthropogenic variables has not been compared. Using data from hundreds of lakes in Ontario Canada, the first objective of this study was to determine which indicator best reflected underlying patterns in regional and local ecological (air temperature, precipitation, lake morphometry and water quality) and anthropogenic (watershed stress from human activities and angling pressure) variables. We hypothesized that because NLSS slope is calculated using measures of both body size and CPUE, more of the variation in NLSS slope will be explained by the ecological and anthropogenic factors than body size and CPUE alone. The second objective of our study was to determine the relative influences of regional versus local ecological and anthropogenic variables on the indicators, and assess responses of the indicators to the ecological and anthropogenic gradients. We hypothesized that a combination of regional and local variables would have greater influence on mean body size, CPUE and NLSS slope than regional or local factors alone. For example, thermal habitat quality and quantity that influence fish growth (body size) and abundance are influenced by large-scale patterns in air temperature and small-scale patterns in lake morphometry. We also hypothesized that air temperature, lake area and angling pressure would be among the most influential variables. They have been shown to influence body sizes and densities of different species in lakes (Lester et al. 2004; Emmrich et al. 2014) and directly impact fish assemblages via size-selective mortality.

Methods

Study area

There are approximately 50,000 lakes with surface areas >50 ha dotting the ~920,000 km² landmass of Ontario (OMNR 2012). Climate varies across the landscape with mean annual

air temperatures ranging from -5 °C in the north to 9 °C in the south, and precipitation varying regionally from 400 to 1,000 mm per year with more in the lee of the Great Lakes. Land cover surrounding the lakes varies from pristine, undisturbed forested watersheds in the north to urbanized, industrial watersheds in the south (Baldwin et al. 2000; Crins et al. 2009).

Data

Several datasets were compiled for 693 lakes dispersed across Ontario to determine which indicator; mean size, CPUE or NLSS slope, best reflects regional and local ecological and anthropogenic conditions, and the relative influences of those variables on the indicators (Fig. 2). Lakes were sampled using Ontario Ministry of Natural Resources and Forestry's (OMNRF) Broad-scale Fish Community Monitoring (BsM) protocol (Sandstrom et al. 2011). Standardized surveys were conducted to gather data on water quality, fish assemblages, and angling pressure in each lake (Sandstrom et al. 2011). Spatial analyses described below, which were required to estimate values for some of the variables, were performed in ArcGIS® (version 10.1 ESRI, Redlands, California).

Ecological variables

Regional ecological variables in our study were degree days, precipitation, and total dissolved solids concentration. The Ontario Ministry of Natural Resources (OMNR) Historical Climate Analysis Tool (Cross et al. 2012) was used to join the centroids of each lake polygon to 1981-2010 climate normals of degrees days above 5°C and total precipitation (Table 1). Degree days were used as the descriptor of air temperature instead of mean or maximum air temperature because it has been empirically linked to fish species distributions and biomass in Ontario (Lester et al. 2004; Chu et al. 2005). Total dissolved solids concentration was our measure of regional water chemistry because it reflects broad-scale differences in surficial geology; the

Precambrian rock of the Canadian Shield in central Ontario and sedimentary rocks in southern and northern Ontario (Baldwin et al. 2000). The different chemistry and weathering characteristics of these geological types consequently affect the physical, chemical and biological characteristics of their waterbodies (Baldwin et al. 2000; Neff and Jackson 2013). Total dissolved solids were analyzed using water samples collected in each lake via the BsM protocol (Sandstrom et al. 2011; Palmer et al. 2011).

Local, lake-scale ecological variables were lake surface area, maximum depth, mean depth, proportion littoral area, pH, true colour, and Secchi depth (Table 1). Lake area and depth variables were compiled from the OMNR Aquatic Habitat Inventory (AHI) (Dodge et al. 1985). Hypsographic curves from the AHI data were used to calculate the proportion littoral area; lake surface area shallower than 4.6 m as defined in Pierce and Tomcko (2005) (Table 1). Secchi depths and water samples were acquired from each lake in spring (Sandstrom et al. 2011) and analyzed for their chemical composition using the protocol outlined in Palmer et al. (2011). Day of year on which sampling took place was also recorded for each lake (Table 1).

Anthropogenic variables

Anthropogenic variables were summarized using watershed stress; a regional index of human activities, and angling pressure; a local estimate assumed to be an indicator of fisheries exploitation in each lake. The watershed stress index summarizes the densities of crop farms, forestry operations, petroleum manufacturing, waste management, human dwellings, air discharge sites, and road densities in Ontario's tertiary watersheds (Chu et al. 2015). ArcGIS® was used to calculate the tertiary watershed stress index of each lake using spatial joins (Table 1).

Angling pressure was measured as part of the BsM protocol. Aerial surveys of angler activities in summer (8 weekday and 8 weekend flights) and winter (6 weekday and 6 weekend flights) provided the data used to estimate annual angling pressure (Table 1). The summer count included the number of vessels and shore anglers whereas the winter count included the number of ice huts and anglers on open ice. Weekend and weekday angler counts were used to calculate mean angling activity for each season in each lake i :

$$Activity_{i,s,m} = \frac{5/\overline{count}_{weekday,i,s,m} + 2/\overline{count}_{weekend,i,s,m}}{Area_i} \quad (1)$$

where s is season (summer or winter), m is method of angling (vessels, shore angler, ice hut, open ice angler), $count$ is number for each method, $Area$ is the lake surface area (ha), and $Activity_{i,s,m}$ is the mean seasonal activity (count·ha⁻¹) for each method in each lake. $Activity_{i,s,m}$ is then multiplied by the number of anglers in vessels, shore angler, ice hut, open ice angler, season length and hours fished per day then summed for all seasons and methods to produce annual estimates of angling pressure:

$$Ang_i = \sum_{s,m=1}^{s,m} Activity_{i,s,m} \times angler_m \times season \times hours \quad (2)$$

where Ang_i is annual angling pressure (angler·hr·ha⁻¹) in lake i , $angler_m$ is the mean number of anglers for each method, $season$ is season length (days) and $hours$ is hours fished per day (hr·day⁻¹) (Table 2).

Fish community sampling

Fish assemblages were sampled using small and large mesh gillnets. Small mesh gangs were 12.5 m in length with 5 panels of mesh ranging from 13 to 38 mm in stretched mesh (i.e. 13, 19, 25, 32, and 38 mm). Large mesh gangs followed the North American standard (Bonar et

al. 2009): 24.8 m in length with 8 panels of mesh ranging from 38 – 127 mm (38, 51, 64, 76, 89, 102, 114, and 127 mm). Nets were set in the afternoon and lifted in the morning with a target soak time of 18 hours. Typically, a double gang strap was used (i.e. 2 nets strung together).

Sampling was depth stratified and both gears were fished in the following depth strata: 0-3, 3-6, 6-12, and 12-20 m. Sampling sites were assigned randomly within each stratum. The number of sites per stratum ranged from 2 to 9 depending on lake size (see Table 4 in Sandstrom et al. 2011). Approximately 50% of sampled lakes were less than 20 m deep. For deep lakes, the deepest stratum (i.e. > 20 m) typically accounted for less than 25% of a lake's benthic area.

When processing the catch, species and fork length were recorded for all fishes. Day of the year on which netting occurred was also included as a lake characteristic because in theory, netting later in the summer could capture more, small young-of-year fishes. Species richness (number of species caught) were also summarized for each lake from the fish community netting data (Table 1).

Indicators: mean size, catch-per-unit-effort and normalized length size spectrum slopes

Five indicators were analyzed in this study. Mean body sizes of all fishes caught in the small and large mesh nets, total CPUE in the small and large mesh nets, and NLSS slope. Mean fork lengths of all fishes caught (i.e., full range of body size) in the small and large mesh gillnets were calculated to produce two estimates of mean body size for each lake; small mesh mean fork length (FL_S) and large mesh mean fork length (FL_L). In essence, FL_S represented the mean size of small-bodied fish species or young of large-bodied species whereas FL_L represented the mean size of large-bodied species. Selectivity of the gear are unknown at this time, so fishes greater than 210 mm in length (largest size of small-bodied species caught in nets) were removed from the small mesh catch data.

Catch-per-unit-effort was calculated as area-weighted estimates of CPUE for both the small and large mesh gillnets. For each lake, we calculated the CPUE and benthic area in each sampled depth stratum, and then calculated the area-weighted mean. Total small mesh CPUE, $CPUE_S$, and total large mesh, $CPUE_L$, were calculated across the full range of body sizes caught in each lake.

Normalized length size spectrum slopes, which in our study, represent the relationship between size (measured as fork length) and abundance (measured as CPUE), were calculated using what we termed the ‘2-point method’. For this method, the mean (± 1 standard deviation) fork lengths were calculated for the small and large meshes for all 693 lakes. This yielded size intervals of 120 ± 50 mm and 410 ± 150 mm, for the small and large mesh respectively (Fig. 1). This procedure standardized the range of fork lengths upon which the NLSS slopes were calculated to improve comparability i.e., remove the effects of abnormally small or large fishes occasionally caught in the nets. The NLSS slope for each lake i was then estimated from the straight-line linking the two log-transformed size-CPUE coordinates, i.e.:

$$NLSS_i = \frac{\log_2 \left(\frac{CPUE_{i,L,\overline{FL}_{L_i} \pm SD_L}}{2SD} \right) - \log_2 \left(\frac{CPUE_{i,S,\overline{FL}_{S_i} \pm SD_S}}{2SD} \right)}{\log_2(\overline{FL}_{L_i}) - \log_2(\overline{FL}_{S_i})} \quad (6)$$

where $CPUE_{i,L,\overline{FL}_{L_i} \pm SD_L}$ and $CPUE_{i,S,\overline{FL}_{S_i} \pm SD_S}$ are the area-weighted CPUE within the standardized range of body size for the large (260-560 mm; size bin = 300 mm or 2SD) and small (70-170 mm; size bin = 100 mm or 2SD) mesh, and $\overline{FL}_{L_i}$ and $\overline{FL}_{S_i}$ are the midpoints of the size bins (120 and 410 mm for the small and large mesh, respectively) within lake i (Fig. 1). This index is not intended to be an accurate estimate of the true size spectrum slope, as differences in catchability and size selectivity between large and small mesh types were not included because at this time,

the selectivity of the small mesh gear is unknown. However, because the two mesh types are designed to catch fish within different size ranges, with little overlap, it is expected to be a monotonic function of the true spectrum and represent in a useful manner, the relative contribution of small versus large organisms in a community.

Statistical analyses

Descriptive statistics were calculated for each ecological and anthropogenic variable (Table 1). Variables that were highly skewed (skewness values ≥ 1.5) were transformed to attain normality for further analyses. A Pearson correlation matrix was used to identify highly correlated variables ($r < -0.6$ or > 0.6) (SPSS 2000). When two variables were highly correlated, one was removed at random, and when one variable was highly correlated with two or more variables, it was retained and the other two excluded. Consequently, maximum depth, proportion of littoral area, pH, true colour, and species richness were removed from further analyses (Table 3).

Boosted regression tree analyses (BRT) were used to identify which variables influenced mean size, CPUE and NLSS slopes, the relative influence of each variable, and percentage deviance of the indicators explained by the BRT models. Boosted regression trees combine regression trees (generated with recursive binary splits) with boosting (combining trees to improve predictive performance) to produce a model built on multiple instead of single trees (Elith et al. 2008). The general approach is to iteratively compute a sequence of trees, where each successive tree is built from the prediction residuals of the preceding tree. The optimal number of trees is determined when the mean predictive deviance of the 10-fold cross validation process is minimized given the learning rate, tree complexity and bag fraction settings. Deviance measures how much the predicted values differ from the observations and represents the loss in

predictive performance due to a suboptimal model. Percentage deviance explained, or pseudo- R^2 , was calculated as $1 - (\text{residual deviance} / \text{total deviance})$ and similar to traditional regression techniques, should approach one when predictive performance is maximized (Elith et al. 2008). The 10-fold cross-validation process evaluates predictions of the model using ten subsets of randomly selected data (Emmrich et al. 2014). The minimum number of trees recommended by Elith et al. (2008) is 1000 to reduce the influence of a single tree on the final model.

Relative influences of the explanatory variables are determined based on the number of times they are included in the trees, and the improvement in the models with their inclusion, averaged across all trees (Friedman and Meulman 2003; Elith et al. 2008). They are scaled to 100 with higher numbers indicating stronger influences on the response variables (Elith et al. 2008). The BRT models were developed with Gaussian error distributions, learning rates of 0.01, 0.05, and 0.001, tree complexities of 2-4, and bag fractions of 0.5 and 0.75. The simple statistics were performed using XLSTAT (Addinsoft 2014). The BRT models were developed using the 'dismo' and 'gbm' packages in R 2.15 (R Core Team 2014) as outlined by Elith et al. (2008).

Results

Species richness in the lakes ranged from 2 to 24. Lakes in northwestern and southern Ontario had greater biodiversity than lakes in central Ontario (Fig. 3). The most common large-bodied species caught in the lakes were white sucker *Catostomus commersoni*, which were found in 680 of the 693 lakes followed by northern pike *Esox lucius* (534 out of 693), and walleye *Sander vitreus* (504 out of 693). The most common small-bodied species were yellow perch *Perca flavescens*, which were caught in 616 of the 693 lakes and cisco *Coregonus artedii* caught in 422 of the 693 lakes (Appendix A). Thirty-one of the 87 species were found in less than 10 of the 693 lakes. Fish assemblages in northern Ontario had higher proportions of coldwater species

than fish assemblages in southern Ontario. Coolwater species were common across the province (Fig. 3).

All of the BRT models developed for mean size, CPUE and NLSS slope were run with tree complexities of 4, learning rates of 0.001 and bag fractions of 0.5. The number of optimal trees ranged from 1700 to 6850 trees depending on the indicator. Fork lengths for all fishes caught in the small mesh nets ranged from 30 to 210 mm. Mean fork lengths (FL_S) ranged from 50 mm to 165 mm (Table 4). Fork lengths of fishes caught in the large mesh gillnets ranged from 120 to 1300 mm with mean fork lengths (FL_L) with means of 256 mm to 557 mm (Table 4). Total small mesh CPUE varied more than large mesh CPUE with the former ranging from 1.8 to 1405 fishes·100m-night⁻¹ and later ranging from 0.4 to 98.9 fishes·100m-night⁻¹. Normalized length size spectra (NLSS) slopes ranged from -5.6 to 1.1 (Table 4).

Boosted regression tree models explained more deviance in large mesh CPUE and NLSS slope than the other indicators (Table 5). Models that combined regional and local variables explained more percentage deviance in the indicators than models based on regional or local variables alone. At the regional scale, NLSS slope was more strongly related to the explanatory variables than mean body size or CPUE indicators. At the local and combined scale, the models explained more deviance in the large mesh CPUE than any other indicator (Table 5).

The relative influences of the variables differed among indicators, and the responses of the indicators to those variables varied (Fig. 4). Ecological variables had greater influence on the indicators than the anthropogenic variables but the relationship was not strong because angling pressure was the second most influential variable affecting NLSS slope and third most influential for small mesh CPUE and large mesh mean fork length (Fig. 4). Watershed stress had little impact on any of the indicators.

In general, fishes caught in small mesh gillnets were larger in big, dark lakes located in wet, warm climates sampled earlier in the year than small, clear lakes in cool, dry climates sampled later in the year (Fig. 4). Large lakes in dry climates with intermediate TDS levels and low angling pressure had larger fishes than small lakes with high TDS in wet climates (Fig. 4). Lakes with high TDS in cool climates and with low or high levels of angling pressure had higher densities of small-bodied fishes than warm lakes with low TDS and intermediate levels of angling pressure (Fig. 4). Large, shallow lakes in dry, cool climates with more TDS had higher densities of large fishes than small, deep, clear lakes (Fig. 4). Large lakes in dry, cool climates with intermediate levels of angling pressure had shallower NLSS slopes than small lakes in wet, warm climates with no or high levels of angling pressure (Fig. 4).

Discussion

The species richness and thermal diversity patterns reflect the biogeography and air temperature trends in Ontario. Higher species richness in the northwest and south can be attributed to postglacial re-colonization stemming from the Mississippian and Atlantic Coastal refugia (Mandrak and Crossman 1992). Mandrak (1995) found that regional lake species richness in Ontario was correlated with length of time since deglaciation, length of time covered by glacial lakes, distance from dispersal corridor, and mean annual air temperature. In a study of 9,679 lakes, Minns (1989) highlighted that historical, regional (watershed species richness, elevation), and local (lake area and mean depth) factors influence lake-level species richness in Ontario.

The thermal diversity of the fish assemblages is consistent with latitudinal changes in mean annual air temperature in Ontario (-5 °C in the north to 9 °C in the south (Crins et al. 2009)), and the positive correlation between air temperatures and water temperatures in lakes

(e.g., Shuter et al 1983). Coolwater species were abundant throughout the province but the southern boundaries of many coldwater species ranges and northern boundaries of many warmwater species ranges intersect in Ontario (Mandrak and Crossman 1992; Jackson et al. 2001).

Informative indicators for fish assemblages should represent causal ecological processes, be sensitive enough to show patterns across the landscape, and reflect underlying conditions that influence those patterns e.g., gradients of climate or morphometry (Cairns et al. 1993; Karr and Chu 1997; Mark et al. 2003). Therefore, the best indicator would be the one with the most percentage deviance explained by the underlying regional and local explanatory variables. All of the indicators varied across the province and reflect ecological processes of body size (FL_S and FL_L), habitat-community production dynamics ($CPUE_S$ and $CPUE_L$), and/or trophic dynamics and energy transfer (NLSS slope) (although these are not mutually exclusive). We hypothesized that because NLSS slope is calculated using measures of both body size and CPUE; both demonstrated indicators for fish assemblages (e.g., Emmrich et al. 2014), it would be the best indicator. Indeed 56.5% (45% for cross-validation dataset) of the variation in the NLSS slopes were related to the explanatory variables used in our study, but 57.7% (46.1% cross-validation dataset) of the variation in large mesh CPUE was explained by the variables. These results suggest that large mesh CPUE and NLSS slopes are good indicators for Ontario's inland lakes. Small mesh mean fork length was the worst indicator because only 26.1% (20.4% cross-validation dataset) of the deviance was related to the explanatory variables. Our results support previous research indicating that larger organisms are more sensitive to environmental conditions and perturbations (e.g., habitat degradation or exploitation) than smaller organisms (Jennings and Dulvy 2005; Shin et al. 2005). Additionally, large-sized organisms should be less affected by

short-term stochastic recruitment fluctuations expected to be more common among smaller size classes and therefore show patterns at the scale of this study better than smaller size classes.

We hypothesized that BRT models with both regional and local variables would explain more deviance in the indicators than regional or local models alone because of the complexity of ecological processes that affect growth, habitat, population and community dynamics. We also hypothesized that air temperature, lake area, and angling pressure would be among the most influential variables. The results supported our first hypothesis but the relative importance of air temperature, lake area, and angling pressure were not consistent among indicators. Below, we summarize the responses and mechanisms by which the variables affect large mesh CPUE and NLSS slopes; the indicators best described by the models, to improve our understanding of the drivers affecting body size, density, and community dynamics in lake fish assemblages.

Large mesh CPUE was influenced by (in descending order) lake area, mean depth, precipitation, TDS, degree days, Secchi depth, day of year, angling pressure, and watershed stress. Large lakes had larger fishes and higher densities of large fishes than small lakes. These results support the *ecosystem size hypothesis*, which states that increased habitat availability and heterogeneity in large systems, lowers omnivory and increases dietary specialization. This results in longer food chain lengths that include new large-bodied, top predators (Post et al. 2000; Griffiths 2013).

Lower large mesh CPUE with increasing mean depth suggests that densities of large fishes were less in deep lakes than shallow lakes. Lake area and mean depth were not correlated for the 693 lakes included in this study ($r = 0.25$), but mean depth was negatively correlated with the proportion of littoral habitat available in the lakes ($r = -0.75$). In Ontario, littoral habitats generally support many large-bodied warmwater and coolwater species e.g., northern pike (*Esox*

lucius), smallmouth bass (*Micropterus dolomieu*), and largemouth bass (*Micropterus salmoides*) therefore, the decrease in large mesh CPUE with increases in mean depth may be due to the absence or fewer large-bodied littoral species in lakes with less littoral habitat.

Large mesh CPUE was higher in lakes in dry, cool climates than lakes in wet, warm climates. This was related to the decline in body size in wet, warm climates making fishes less vulnerable to the large mesh gear. In Ontario, air temperatures decrease with latitude and precipitation increases with longitude, especially in regions leeward of the Great Lakes that receive lake effect precipitation. Precipitation is an integral part of the water budgets of lakes but the mechanisms directly linking precipitation to fish assemblage dynamics require further investigation. The mechanisms by which temperature affects fish populations and assemblages are better understood. Emmrich et al. (2014) attributed the decrease in mean size of fish assemblages in 356 European lakes with increasing temperatures to the *temperature-size rule* whereby increases in developmental temperature can lead to decreases in adult body size in ectotherms. Rypel (2014) found that *Bergmann's Rule*, which states that body size correlates positively with latitude and negatively with temperature, is upheld for coolwater and coldwater fishes, but the opposite is true for warmwater fishes. In Ontario and Quebec, walleye in the south attain smaller body sizes than walleye in the north because they do not live as long in warmer climates (Venturelli et al. 2010). Lake trout populations exposed to longer, warmer winters have smaller maximum sizes than lake trout in colder climates (McDermid et al. 2010), and yellow perch maximum body size is positively related to lake size and negatively related to degree days (Purchase et al. 2005). For warmwater species in cold climates, long winters necessitate the need to accumulate storage, which can lead to hampered growth and smaller sizes of warmwater species (Giacomini and Shuter 2013).

The decline in large mesh CPUE in wet, warm climates is also a product of the fish assemblages present in southern Ontario lakes. Warmwater species comprised more than 50% of the fish assemblages in southern lakes but many of these species; e.g., pumpkinseed (*Lepomis gibbosus*), rock bass (*Ambloplites rupestris*), and bluegills (*Lepomis macrochirus*) do not grow as large as coolwater or coldwater percids and trout, and are therefore less vulnerable to the large mesh gear.

Secchi depth and TDS concentration are recognized nutrient availability and water quality indicators for lakes. In our study, large mesh CPUE was low in clear-low TDS lakes but high in dark-high TDS lakes. Secchi depth and TDS were not strongly correlated for the 693 lakes ($r = -0.02$) but low Secchi depths correspond to high nutrient availability. Therefore, lakes with more essential nutrients and minerals have higher CPUE. Positive relationships between Secchi and/or TDS and fish biomass and production are well-explored in the literature (Ryder et al. 1974; Prepas 1983; Downing and Plante 1993; Purchase et al. 2005).

It was expected that watershed stress and angling pressure would reduce large mesh CPUE because larger organisms are more sensitive to environmental perturbations and harvest than smaller organisms (Leach et al. 1987; Jennings and Dulvy 2005; Shin et al. 2005). Large mesh CPUE did decline at angling pressures greater than ~ 15 angler-hr-ha⁻¹, but our results suggest that it is not a good indicator of patterns in anthropogenic variables because across the broad scale of our study, the ecological variables were more important.

The NLSS slopes provided a simple measure of both small and large-bodied fishes, and were influenced by (in descending order) precipitation, angling pressure, degree days, TDS concentration, lake area, secchi depth, watershed stress, mean depth and sampling day of the year. The responses of the slopes along gradients of the five most influential variables are

described in Fig. 5. Slope was most sensitive to changes in CPUE (y -axis) because body size values used for its calculation were constrained to be within fixed size bins (Equation 6 and Fig. 1). Lakes in wet, warm climates had steeper slopes than lakes in comparatively dry, cool climates. This pattern was driven by decreases in large mesh CPUE i.e., large mesh side of NLSS slope relationship decreased (Fig. 5). A similar pattern was found in 356 lakes across Europe (Emmrich et al. 2014), and these patterns can be partially (partial because understanding the precipitation effect requires further research) attributed to temperature effects on fish size discussed previously.

Slopes increased from 0 to ~ 7 angler-hr-ha⁻¹ but decreased once angling pressure was > 7 angler-hr-ha⁻¹. Steep slopes in lakes with no angling pressure or < 7 angler-hr-ha⁻¹ were unexpected. In some of these lakes, steep slopes may exist because of historical but now defunct angling pressure. Further research could incorporate 'fishery age' into the models and can be estimated using the chronological expansion of cities and towns or road networks because in Ontario, angler effort increases with proximity to residences and roads (Hunt et al. 2011). At angling pressures > 7 angler-hr-ha⁻¹, NLSS slopes were steeper as a result of decreases in large mesh body size, increases in small mesh CPUE, and decreases in large mesh CPUE (Fig. 5). This pattern has been observed in other fisheries where harvest of large-bodied species resulted in reductions in the size and/or abundance of large-bodied fishes and prey releases of small-bodied fishes (increased CPUE_s) (Shin et al. 2005; Sweeting et al. 2009).

The NLSS slopes were steeper in lakes with high TDS concentrations and shallower in large versus small lakes. Steeper NLSS slopes at high TDS concentrations were due to increases in small and large mesh CPUE. Shallower slopes in large lakes were due to the presence of more large-bodied fishes in large versus small lakes for reasons mentioned above (Fig. 5).

A noteworthy pattern that emerged from the indicators was the presence of ‘bumps’ – increases followed by decreases in the indicators between 1400 and 1800 degree days. These bumps reflect thermal habitat. Ascending limbs of the ‘bumps’ reflect the entrance of warmwater species into the small and large mesh catch while the descending limbs reflect the exit of coldwater species and perhaps some coolwater species at warmer temperatures.

Greater than 50% of the variation in large mesh CPUE and NLSS slopes were explained by the regional and local variables. These values are similar to those observed for 356 lakes across Europe in which Emmrich et al. (2014) related fish mean body size to fish assemblage, maximum air temperature and maximum depth (30.2%), and size spectrum slope to fish assemblage, maximum air temperature and lake area (46%). One significant difference between the two regions was the influence of lake size on slope; steep slopes in large lakes in Europe (Emmrich et al. 2014) versus shallow slopes in large lakes in Ontario. This difference may be related to fish assemblage differences. In Ontario, 87 unique species were caught whereas 54 species were caught in Europe. The Ontario dataset also included large-bodied cool and warmwater species such as smallmouth bass *Micropterus dolomieu*, white sucker *Catostomus commersoni* and redhorses *Moxostoma* sp. not found in the European study.

The NLSS slopes in our study were developed using a 2-point method; linear slopes between mean FL_S -mean $CPUE_S$, and mean FL_L -mean $CPUE_L$, and represented relative instead of absolute measures of NLSS slope. All of the NLSS slopes (-5.6 – +1.1) were shallower than the expected value of -6, which suggests that the 2-point method could be underestimating mean FL_S -mean $CPUE_S$ while overestimating mean FL_L -mean $CPUE_L$. Future research to determine the selectivity of the gears and inclusion of that selectivity may correct this, and would refine all of the estimates for our indicators. Slopes derived from all size classes as opposed to the mean

FL_S and mean FL_L may be steeper than our NLSS slopes. Inclusion of lower trophic levels (phytoplankton and zooplankton) may also refine the NLSS slope estimates. Nevertheless, consistencies between our results and studies on European lakes across broad geographic regions (Emmrich et al. 2011; Emmrich et al. 2014) lend support for the 2-point method.

Our results highlight that indicators developed from small-bodied organisms are not as sensitive to broad-scale environmental gradients as large-bodied organisms and indicators that incorporate CPUE describe the variation among lakes better than mean body size indicators. This study is the first size-based and catch-based indicator study, to our knowledge, to include detailed observations of direct angling pressure on hundreds of inland lakes. In general, ecological variables explained more variability in the indicators and multi-scale models performed better than models with regional or local variables alone. These results reveal the complexity of indicator responses to regional and local variation in ecological and anthropogenic conditions.

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Table 1. Characteristics of 693 lakes in Ontario used to determine the influence of regional and local ecological and anthropogenic variables on commonly used ecological indicators for fish assemblages; mean body size, catch-per-unit-effort, and normalized length size spectrum slopes. SD is standard deviation.

Variable	Abbreviation	Mean±SD	Median	Range
Degree days above 5°C	Dd5	1617±213	1614	1059-2246
Precipitation (mm)	Pcp	827±107	815	599-1157
Total dissolved solids (mg·L ⁻¹)	TDS	47.7±48.3	31.8	1-394.9
Watershed stress from human activities (range; 0-1)	Stress	0.18±0.07	0.17	0-0.58
Lake surface area (ha)	Area	2113±6391	615	21-90484
Maximum depth (m)	Depmx	30±24	23.0	1-213.5
Mean depth (m)	Depmn	8.7±6.7	6.9	0.6-40.1
Proportion littoral area	Plitt	0.46±0.23	0.42	0.06-1
pH	pH	7.2±0.5	7.1	5.61-8.7
True colour	TCU	38.6±30.2	29.6	2.6-166
Secchi depth (m)	Secchi	3.6±1.8	3.3	0.3-12
Annual angling pressure (angler-hr·ha ⁻¹)	Ang	7.44±12.88	3.44	0-182.7
Sampling day of year	Day	208±28	208	94-283
Fish species richness	Spp	11±4	11	2-24

Table 2. Factors used to convert angler activity counts to estimates of annual angling pressure (angler-hr·ha⁻¹) on 693 Ontario lakes used to investigate the change in mean size, catch-per-unit-effort, and normalized length size spectrum slopes along broad gradients of environmental conditions and angling pressure.

Season	Angler activity (count·ha ⁻¹)	Mean number of anglers per fishing method	Season length (days)	Number of hours fishing per day
Summer	Vessel	2	150	12
Summer	Shore	1	150	12
Winter	Ice hut	2	90	8
Winter	Open ice	1	90	8

1 Table 3. Pearson correlations among variables used to determine the influences of regional and local ecological and anthropogenic
2 variables on ecological indicators for fish assemblages in 693 Ontario lakes. Stress was arcsin squareroot transformed to attain
3 normality. Abbreviations are defined in Table 1.

	<i>Dd5</i>	<i>Pcp</i>	<i>log₁₀</i>	<i>Stress</i>	<i>log₁₀</i>	<i>log₁₀</i>	<i>log₂</i>	<i>Plitt</i>	<i>pH</i>	<i>TCU</i>	<i>Secchi</i>	<i>Day</i>	<i>Spp</i>	<i>log_{10(x+1)}</i>
			<i>TDS</i>		<i>Area</i>	<i>Depmx</i>	<i>Depmn</i>							<i>Ang</i>
<i>Dd5</i>	1.00													
<i>Pcp</i>	0.52	1.00												
<i>log₁₀TDS</i>	0.23	0.14	1.00											
<i>Stress</i>	0.50	0.48	0.10	1.00										
<i>log₁₀Area</i>	-0.04	-0.21	0.17	-0.12	1.00									
<i>Log₂Depmx</i>	0.10	0.05	-0.16	0.06	0.38	1.00								
<i>log₂Depmn</i>	0.13	0.04	-0.16	0.05	0.25	0.91	1.00							
<i>Plitt</i>	-0.15	-0.05	0.16	-0.06	-0.18	-0.75	-0.91	1.00						
<i>pH</i>	0.08	-0.06	0.86	0.01	0.19	-0.21	-0.22	0.19	1.00					
<i>TCU</i>	-0.31	-0.28	-0.13	-0.24	0.03	-0.37	-0.43	0.41	-0.12	1.00				
<i>Secchi</i>	0.21	0.22	-0.02	0.18	0.00	0.46	0.52	-0.47	-0.04	-0.68	1.00			

<i>Day</i>	-0.02	-0.01	-0.02	-0.04	0.03	0.01	0.00	0.03	-0.08	0.01	-0.07	1.00		
<i>Spp</i>	0.40	0.07	0.29	0.10	0.60	0.36	0.31	-0.29	0.23	-0.20	0.11	-0.01	1.00	
<i>log_{10(x+1)}Ang</i>	0.55	0.49	0.39	0.32	0.07	-0.04	-0.04	0.01	0.25	-0.23	0.08	-0.01	0.31	1.00

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Table 4. Descriptive statistics of mean body size, total catch-per-unit-effort, and normalized length size spectrum slopes of fish assemblages in 693 lakes in Ontario sampled using standardized protocols with small and large mesh gillnets. SD is standard deviation.

Ecological indicator	Abbreviation	Mean±SD	Median	Range
Small mesh mean fork length (mm)	FL _S	97±20	96	50-165
Large mesh mean fork length (mm)	FL _L	385±51	386	256-557
Small mesh catch-per-unit-effort (number·100m-night)	CPUE _S	170.5±172.6	96.1	1.8-1405.2
Large mesh catch-per-unit-effort (number·100m-night)	CPUE _L	23.5±16.4	19.2	0.4-98.9
Normalized length size spectra slope	NLSS slope	-2.2±1.2	-2.1	-5.6-1.1

Table 5: Percentage deviance explained using boosted regression tree analyses to examine the influence of regional (degree days, precipitation, water chemistry, watershed anthropogenic stress) and local (lake morphometry, water quality, angling pressure and sampling day of year) variables on ecological indicators; mean body size, total catch-per-unit-effort, and normalized length size spectrum slopes of fish assemblages in 693 Ontario lakes. Values in brackets represent percent deviances explained of the cross-validation datasets.

Scale	Small mesh mean fork length	Large mesh mean fork length	Small mesh catch-per- unit-effort	Large mesh catch-per- unit-effort	Normalized length size spectrum
Regional	12.5 (3.4)	36.8 (23.9)	35.7 (20.0)	36.5 (22.1)	40.5 (24.1)
Local	13.6 (4.5)	29.0 (7.9)	15.6 (3.7)	44.2 (28.8)	33.5 (21.9)
Regional and local	26.1 (20.4)	44.7 (34.2)	48.9 (31.1)	57.7 (46.1)	56.5 (45.0)

Figures

Fig. 1. Schematic of expected slopes for normalized size spectra calculated using different measures of body size and abundance. Bars and dotted line illustrate how normalized length size spectrum slopes were calculated in our study from ranges of small and large mesh catch data from fish assemblages sampled in 693 lakes in Ontario. SD is standard deviation.

Fig. 2. Locations of 693 lakes sampled in Ontario to compare mean size, catch-per-unit effort, and normalized length size spectra as indicators of fish assemblages along gradients of regional and local ecological and anthropogenic variables.

Fig. 3. Fish species richness and proportion of assemblage with b) coldwater, c) coolwater, or d) warmwater thermal preferences in 693 Ontario lakes used to compare mean size, catch-per-unit effort, and normalized length size spectra as indicators of fish assemblages along gradients of regional and local ecological and anthropogenic variables.

Fig. 4. Partial dependence plots generated from boosted regression tree analyses showing the responses of ecological indicators of lake fish assemblages to regional and local ecological and anthropogenic variables; FL_S is the mean size of fishes caught in small mesh gear, FL_L is the mean size of fishes caught in large mesh gear, CPUE is the total catch-per-unit-effort in the small mesh gear $CPUE_S$ or large mesh gear; $CPUE_L$, NLSS slope is the normalized length size spectrum slope. Rug plots on the bottom horizontal axis of each partial dependence plot show the distributions of the variables in deciles. Bar graphs show the relative influences of the variables on the indicators.

Fig. 5. Change in normalized length size spectrum slopes in response to changes in the five (a-e) most influential regional and local ecological and anthropogenic variables (Fig. 4). Vertical arrows indicate changes in catch-per-unit-effort (CPUE) whereas horizontal arrows indicate changes in fork length. Slope is most sensitive to changes in CPUE because the body size values used for its calculation were constrained to be within fixed size bins (Equation 6 and Fig. 1). Changes in the slopes are for illustration purposes and are not to scale but wider arrows indicate greater changes than thinner arrows. For example, as precipitation increases, the change in slope is the cumulative function of large mesh CPUE decreasing, large mesh mean fork length getting smaller, and small mesh mean fork length getting larger, which leads to an overall steepening of the slope.

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Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Appendix A: Occurrences and thermal preferences of 87 fish species captured in 693 Ontario lakes sampled as part of the Ontario Ministry of Natural Resources and Forestry Broad-scale Fish Community Monitoring program.

Species	Scientific	Thermal class	Number of lakes
cisco	<i>Coregonus artedii</i>	cold	422
lake whitefish	<i>Coregonus clupeaformis</i>	cold	377
lake trout	<i>Salvelinus namaycush</i>	cold	303
trout-perch	<i>Percopsis omiscomaycus</i>	cold	302
lake chub	<i>Couesius plumbeus</i>	cold	104
longnose sucker	<i>Catostomus catostomus</i>	cold	88
brook trout	<i>Salvelinus fontinalis</i>	cold	81
ninespine stickleback	<i>Pungitius pungitius</i>	cold	65
rainbow smelt	<i>Osmerus mordax</i>	cold	63
mottled sculpin	<i>Cottus bairdi</i>	cold	51
slimy sculpin	<i>Cottus cognatus</i>	cold	51
spoonhead sculpin	<i>Cottus ricei</i>	cold	22
round whitefish	<i>Prosopium cylindraceum</i>	cold	13
deepwater sculpin	<i>Myoxocephalus thompsoni</i>	cold	11
alewife	<i>Alosa pseudoharengus</i>	cold	5
rainbow trout	<i>Oncorhynchus mykiss</i>	cold	5
splake	<i>Salvelinus namaycush x fontinalis</i>	cold	2
chinook salmon	<i>Oncorhynchus tshawytscha</i>	cold	1
pygmy whitefish	<i>Prosopium coulteri</i>	cold	1

threespine stickleback	<i>Gasterosteus aculeatus</i>	cold	1
white sucker	<i>Catostomus commersoni</i>	cool	680
yellow perch	<i>Perca flavescens</i>	cool	616
northern pike	<i>Esox lucius</i>	cool	534
walleye	<i>Sander vitreus</i>	cool	504
spottail shiner	<i>Notropis hudsonius</i>	cool	344
burbot	<i>Lota lota</i>	cool	275
logperch	<i>Percina caprodes</i>	cool	180
emerald shiner	<i>Notropis atherinoides</i>	cool	159
common shiner	<i>Luxilus cornutus</i>	cool	157
golden shiner	<i>Notemigonus crysoleucas</i>	cool	157
blacknose shiner	<i>Notropis heterolepis</i>	cool	127
pearl dace	<i>Margariscus margarita</i>	cool	50
blackchin shiner	<i>Notropis heterodon</i>	cool	49
sauger	<i>Sander canadense</i>	cool	45
northern redbelly dace	<i>Phoxinus eos</i>	cool	42
brook stickleback	<i>Culaea inconstans</i>	cool	40
creek chub	<i>Semotilus atromaculatus</i>	cool	39
Johnny darter	<i>Etheostoma nigrum</i>	cool	39
silver redhorse	<i>Moxostoma anisurum</i>	cool	22
fallfish	<i>Semotilus corporalis</i>	cool	14
lake sturgeon	<i>Acipenser fulvescens</i>	cool	14
mooneye	<i>Hiodon tergisus</i>	cool	14
blacknose dace	<i>Rhinichthys atratulus</i>	cool	13

Iowa darter	<i>Etheostoma exile</i>	cool	13
longnose dace	<i>Rhinichthys cataractae</i>	cool	12
greater redhorse	<i>Moxostoma valenciennesi</i>	cool	10
banded killifish	<i>Fundulus diaphanus</i>	cool	9
central mudminnow	<i>Umbra limi</i>	cool	9
finescale dace	<i>Phoxinus neogaeus</i>	cool	8
hornyhead chub	<i>Nocomis biguttatus</i>	cool	2
quillback	<i>Carpionodes cyprinus</i>	cool	2
river redhorse	<i>Moxostoma carinatum</i>	cool	2
bridle shiner	<i>Notropis bifrenatus</i>	cool	1
brook silverside	<i>Labidesthes sicculus</i>	cool	1
gizzard shad	<i>Dorosoma cepedianum</i>	cool	1
marginated madtom	<i>Noturus insignis</i>	cool	1
round goby	<i>Neogobius melanostomus</i>	cool	1
silver lamprey	<i>Ichthyomyzon unicuspis</i>	cool	1
striped shiner	<i>Luxilus chrysocephalus</i>	cool	1
smallmouth bass	<i>Micropterus dolomieu</i>	warm	341
rock bass	<i>Ambloplites rupestris</i>	warm	311
pumpkinseed	<i>Lepomis gibbosus</i>	warm	208
brown bullhead	<i>Ameiurus nebulosus</i>	warm	144
bluntnose minnow	<i>Pimephales notatus</i>	warm	113
largemouth bass	<i>Micropterus salmoides</i>	warm	108
shorthead redhorse	<i>Moxostoma macrolepidotum</i>	warm	94
black crappie	<i>Pomoxis nigromaculatus</i>	warm	69

bluegill	<i>Lepomis macrochirus</i>	warm	64
mimic shiner	<i>Notropis volucellus</i>	warm	46
muskellunge	<i>Esox masquinongy</i>	warm	44
fathead minnow	<i>Pimephales promelas</i>	warm	42
yellow bullhead	<i>Ameiurus natalis</i>	warm	22
channel catfish	<i>Ictalurus punctatus</i>	warm	14
common carp	<i>Cyprinus carpio</i>	warm	14
longnose gar	<i>Lepisosteus osseus</i>	warm	10
bowfin	<i>Amia calva</i>	warm	9
goldeye	<i>Hiodon alosoides</i>	warm	6
freshwater drum	<i>Aplodinotus grunniens</i>	warm	4
longear sunfish	<i>Lepomis megalotis</i>	warm	4
golden redhorse	<i>Moxostoma erythrurum</i>	warm	3
spotfin shiner	<i>Cyprinella spiloptera</i>	warm	3
green sunfish	<i>Lepomis cyanellus</i>	warm	2
rosyface shiner	<i>Notropis rubellus</i>	warm	2
black bullhead	<i>Ameiurus melas</i>	warm	1
grass pickerel	<i>Esox americanus vermiculatus</i>	warm	1
sand shiner	<i>Notropis stramineus</i>	warm	1
white bass	<i>Morone chrysops</i>	warm	1